THE RELATIONS OF THE RETINAL IMAGE TO ANIMAL REACTIONS.

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During the past generation the interpretation of animal activities has undergone a profound change. To the earlier naturalists even the simplest animals were supposed to be endowed with sensations, preferences, desires, volitions, and the like, which, though simplified in form, were nevertheless the same as those in ourselves. But this so-called anthropomorphic viewpoint was soon found to present many difficulties, some of which turned upon new discoveries concerning man himself. It was becoming apparent gradually that human beings, in addition to their ordinary mental life, possess a multitude of nervous activities, some of which are subconscious and many of which have no direct relation whatever with consciousness. The more these matters were looked into the more evident it became that our conscious activities were limited to a special part of our nervous organization, to the brain and perhaps even to the cerebral cortex, and that much of our nervous system had to do with operations quite free from conscious complications. Thus the heart, the blood vessels, the digestive tube, and other like parts, all of which possess their own nervous equipment, exhibit a range of operations of a highly complex and responsive kind that may be entirely dissociated from our conscious states. As these operations are directed toward the successful continuance of life of the individual in which they occur, we are forced to ask the question, May they not afford an example of the kind of nervous life led by many lower animals whose whole nervous equipment may then be as devoid of the so-called higher nervous states as our heart or our intestines are? An animal thus organized would be merely a delicately adjusted creature without desire, memory, or volition, but responding to changes in its surroundings with as much certainty and precision as our heart or digestive tube does to its environment. To this question much of the evidence of recent years seems to be shaping an affirmative answer.

One of the newer lines of evidence touching on this point has to do with sense organs. These organs are usually regarded as bodily parts concerned with providing us with the elements of information as to the world about us. They are thus intimately associated with our central nervous activities. But they are known to occur in many lowly organized animals, such as the jellyfishes and the like, in which there are no central nervous organs appropriate for such information. In these animals the nervous impulses from the so-called sense organs pass directly to the muscles without first making their way through a central nervous organ. They serve merely as a means of exciting muscular activity and are concerned in no way at all, so far as one can judge, with sensations. Their action is comparable to that of our eye, which, when brightly illuminated, so responds that the muscular sphincter in the iris contracts, thus reducing the size of the pupil. With us sense organs have two functions. They deliver impulses that excite muscles to action, as in the instance just given, and they deliver impulses that serve our central organs in an informing way. Of these two functions only the first is possessed by many of the lower animals. Hence it is without doubt the more primitive, for the second function could not have arisen before the development of a central nervous organ, a part which, as already intimated, is absent from many simple animals.

To the older naturalists the presence of a sense organ was sufficient grounds for assuming that the animal experienced sensations characteristic of that organ. Thus the recognition of eye spots in jellyfishes was supposed to justify the opinion that these animals could see. But from the standpoint of the more recent work the presence of such an organ merely means that the animal is especially responsive to light, not that it has the sensations of sight, for the nervous strands from the eye spot in the jellyfish lead directly to the muscles and not to a central nervous organ. Hence the so-called sense organs of the lower animals, since they are in no necessary way concerned with sensations, are more correctly designated as receptors in consequence of their relation to the stimulus.

Since the so-called sense organs of many of the simpler animals are merely devices for exciting muscle to action, and since many of these animals possess no true central nervous organs, the responses of these admitted, and yet it is also equally clear that these higher animals have been derived from stocks that were purely tropic in their day. How have the tropisms disappeared from these lines of descent and what are the forms of response that represent the transition between tropisms and the diversified movements of the more complex animals? Some insight into the answer to this question can be gained by a comparison of phototropism and vision as elucidated through the retinal image.

It is now well recognized that many of the simpler animals, unicellular as well as multicellular, are extremely responsive to light. The amœba creeps away from a source of illumination, hydra creeps toward it, sea-anemones are for the most part photonegative, earthworms are positive to weak light and negative to strong light, and so forth. In all these simpler animals the surface of the given form is apparently open to stimulation by light in the same sense that our whole skin may be stimulated mechanically for touch. When light falls on an amœba, the formation of pseudopodia ceases on the illuminated side and continues on the side in shadow; hence the animal creatures are of a relatively restricted and circumscribed kind and lack the variety and spontaneity of the reactions of the more complex forms. Such restricted responses are represented by forced movements, or more particularly by tropisms, reaction types characteristic in general of the simpler animals and consisting of rather direct responses of the organism as a whole by moving either toward an obvious source of stimulation or away from it. Such responses, as Loeb has abundantly shown, are the usual types of movements for plants and the lower animals, and, though there is much difference of opinion as to the way in which a tropism is accomplished, there can be no doubt as to its predominance among the reaction forms of the simpler animals.

If, then, tropisms are the common types of response for the simpler animals in which receptors are directly connected with muscles, or at most connect with them through a very primitive kind of central organ, it follows that this type of reaction must underlie that of the more differentiated animals and must have been gradually replaced by the kind of operation that we regard in ourselves as spontaneous and volitional. That there is almost nothing in the responses of the higher animals that recalls a tropism is generally moves away from the light. When sea-anemones are illuminated on one side, the pedal waves begin on that side and spread across the foot to the opposite margin thus carrying the animal, without any previous adjustment to the light, away from the source of illumination. When an earthworm is exposed to bright light it gradually turns its anterior end away from the light and, thus directed, creeps over a negative course. In all these tropic responses the animal falls quickly into line through the influence of the stimulus on the general receptive surface of its body and, without the necessary recourse to specialized organs such as eyes, it takes a direction in relation to the source of disturbance. There is not the least reason to suppose, except possibly in the case of the earthworm, that these activities are indicative of any sensational or other central-nervous element whatever. They are comparable with the movements of our internal organs, such as the heart and the intestine, and from this viewpoint they stand at an equally low and primitive level. They are in every sense forced movements of the tropic variety.

Probably much the same condition obtains in those animals that are provided with the so-called eye spots. These are small photoreceptors found on various places in different animals. They occur on the edge of the bells of jellyfishes, at the ends of the arms of starfishes and around the aboral pole of sea-urchins, on the heads of many worms, of arthropod larvæ, and perhaps of some snails. In typical conditions they consist of a group of receptive cells sunk in an open cup of pigment, so that the receptors are accessible to light only from a generally restricted region, the light from the rest of the field being received by the outer walls of the pigment cup. Such eye spots are unprovided with devices for forming images, either pupils or lenses. Occasionally lenses are present, but when such is the case, the lens is concerned with the concentration of light and not with the formation of an image. Such organs have been appropriately called euthyscopic or direction eyes for the reason that they have to do with light only so far as the direction of its source is concerned and not with the possible formation of images. Animals that possess this type of photoreceptor to the exclusion of other types exhibit perhaps the most striking of all instances of phototropism. The larval stages of many insects are excellent examples of this kind. The maggots of blowflies creep with great precision away from a source of light or take a balanced course between two lights of different intensities or at varying angles of incidence. When one photoreceptor is covered, circus movements result. In short, the animal possessed of direction eyes shows a phototropism that is probably purest in its type in the sense that it is least complicated by extraneous factors.

From the direction eye as a point of departure two chief types of eyes have evolved, both characterized by the capacity to form images. Hence they have been called eidoscopic or image eyes. On the one hand, photoreceptive units, each more or less like a direction eye, have become arranged as a spherical system, thus giving rise to the compound or mosaic eye so common on the optic stalks of crustaceans and on the heads of insects. On the other hand, by enlarging the cavity of the direction eye and providing it with a wall, and a pupil or lens, or both, a camera eye has been produced such as is seen in many snails and higher mollusks like the squids, devilfish, and so forth, and in the vertebrates from fish to man. These two types of eyes produce images that are often remarkably rich in detail, the image in the compound eye being upright and that in the camera eye inverted.

When the light reactions of animals that possess compound eyes, like the insects, for instance, are studied, they are found to be by no means simple tropic responses. The mourning-cloak butterfly, when liberated in a room illuminated by a single, bright light, flies toward the light and behaves in a way to justify the designation positively phototropic. When, however, it is watched in the open field, its reactions are very different. After flying about in the sunlight for a while, these butterflies come to rest definitely oriented to the direction of the sun's rays, but instead of being headed toward the sun, as a positive animal should be, they head away from the sun in the position of negative phototropism. Here, then, is an animal that in flight is positively phototropic, but in its resting posture is negatively so. These two activities, however, are intimately associated with the animal's environment. The flight toward light carries it under natural conditions to sunlit districts, and its negative position when resting in sunlight enables it to display its colors, which in the act of mating is a very important and significant step, as any one can observe in the open field at the appropriate time of year.

Not only is the phototropism of the mourning-cloak butterfly complicated, but the insect exhibits also this peculiarity: that though positively phototropic when in flight, it does not fly toward the sun, the source of strongest light in its natural environment. An experimental test of the animal from this standpoint shows that when it is placed midway between two sources of light of equal intensity, one a small point and the other a large surface, it regularly moves toward the large surface. Under like conditions animals without image eyes keep an even course between the two lights. For the butterfly with eidoscopic eyes the large area of less bright light determines the direction of movements rather than the small area of intense light. Hence in nature these animals fly from one patch of sunlight to another rather than toward the source of all light, and thus they may be said to prefer a place on earth to one in the sun. It takes only a moment's consideration to recognize how complicated the light responses of this butterfly are as compared with those of a purely phototropic animal.

That the reactions of insects to light are built up on a background of phototropic activity seems to the writer to be perfectly clear. The pure phototropic responses are often strikingly exhibited in the larval stages where only direction eyes are present, a condition of affairs pointed out long ago by Loeb in the caterpillars of the Porthesia moth. But they are also easily disclosed in the adult condition, where they are covered at most by a veneer of instinctive activities which represent in reality modified tropic movements such as have been pointed out in the mourning-cloak butterfly. Thus Dolley (1916) has shown that even in the mourning-cloak butterfly itself circus movements may occur on blackening one eye, and the same is true of the still more complex honey bee as studied by Minnich (1919). And Garry (1918) has recently demonstrated in a most striking way the tropic nature of the pose and locomotion in certain flies. Thus the adult insect, though subject to the most diverse movements in an illuminated field, has underlying its whole system of response a basis of simple phototropism. This relation is nowhere better illustrated than in the blowflies. The maggots of these flies are strongly phototropic in a negative sense and exhibit those balanced reactions to opposing lights that are characteristic of the purest form of phototropism. They possess eyes, but these eyes are little more than direction eyes. When they emerge as adults, they have well-developed compound eyes. Under laboratory tests they are said to be positively phototropic, but in the field they exhibit such a variety and complication of photic response as to recall the state of the mourning-cloak butterfly. Bees are without doubt positively phototropic, but their daily life in the illuminated field in which they live is as complex in many respects as that of a human being. As von Frisch (1914) has recently shown, they can be taught to associate color with food supply, and it is impossible to explain their homing instincts without assuming memories, visual and otherwise, of an order fairly comparable with those found in the vertebrates. Thus many insects, though fundamentally tropic in their underlying nervous organization, have built upon this organization an immense superstructure of reaction types mostly of an instinctive kind that obscures and hides the original simple tropic scheme. This overgrowth in phototropism is dependent upon, first, the development of an eidoscopic eye whose image is rich in detail, and, secondly, upon the development of central nervous organs capable of caring for such detail. In this respect the insects offer remarkable transition forms between the purely phototropic simpler organisms and those in which phototropism seems to have vanished completely.

It is a fair question to ask whether vertebrates exhibit any tropic responses whatever. Most students of this subject would answer this question, I imagine, in the negative. Yet it is very difficult to explain, for instance, the feeding habits of the dogfish without assuming a tropic basis. When hungry dogfishes are liberated in a pool in which food is hidden, they begin sweeping the bottom in rapid circular movements, turning now to the right and now to the left. If both nostrils in the fish are closed with plugs of cotton, these movements do not occur. If, now, one nostril is freed, the circular form of locomotion returns with this peculiarity, however, that the circles are now almost always in one direction—*i.e.,* with the free nostril toward the center. Plainly the dogfish scents its food and in hunting turns, as animals exhibiting tropisms do, in the direction appropriate for the more intense stimulus. Thus the dogfish shows responses that in every way have the earmarks of a tropism. This condition, however, is very exceptional, for in general the responses of vertebrates to their environment, as every one knows, resemble vastly more those of the more complex insects than they do the tropic reactions of the simpler organisms.

A remarkable form of vertebrate response in this particular is the instinct shown by newly hatched loggerhead turtles to go toward the ocean. It is a most singular spectacle to see a dozen or more of these newly hatched creatures scramble across the horizontal surface of a wharf directly toward the water which, in consequence of a raised wooden edge, they could not see and with which they had had no previous experience. What determined their direction of motion was at first sight very difficult to say. After some trials, however, it was found that they commonly went away from any large diversified mass, especially when it occupied a part of the horizon line, and they as commonly went toward a uniform and uninterrupted part of the same line. Their first steps in this operation were extremely interesting to watch. When a young turtle is placed in position to move, he quickly raises his head, makes a complete turn through a whole circle to test out apparently his surroundings, and then takes a straight course toward the clearest part of the horizon. That this reaction has of necessity nothing whatever to do with the ocean can be shown by starting the turtle near some high shrubbery, but on the side away from the sea and toward a free, open field. The animal will then move away from the shrubbery and toward the open field with as much certainty as it had previously done toward the water, though in this instance it is plainly moving away from the element which ordinarily it would be expected to seek.

The natural response of the turtle to the sea is so obviously instinctive and so uniform that it presents all the superficial traits of a tropism, but when it is looked into, it appears to be a very precise form of instinctive reaction to the details of the retinal image. When loggerhead turtles were tested in a dark room provided with a single light, they went neither toward the light nor away from it, but remained for the most part quietly resting where they had been put. Contrary to the view expressed by Hooker (1911), they are not phototropic. They are active when their retinal fields are full of detail and they move toward that part of the field in which the horizon is most open. Under natural circumstances this usually brings them to the sea, but it does not necessarily do so, and it is in no sense a true tropic reaction. The young loggerhead turtle exhibits, then, an activity that superficially resembles a tropism, but that in reality is very different. In this respect the animal declares its higher nature.

Most vertebrates respond in very precise ways to the details of their retinal fields. Thus frogs and toads will seize and swallow almost any small moving object, be it a pebble or a bit of wax attached to a string, or a living insect. The motionless insect, like the motionless pebble, escapes. It is something moving in a field otherwise quiescent that excites the reaction. This reaction is dependent, therefore, on a detailed retinal image associated with a highly differentiated central nervous apparatus.

By a strange coincidence a frog through a simple operation may be reduced from an animal responding in the highly complex way just described to one that reacts after the style of pure phototropism. Frogs, like most other animals of their class, are sensitive to light through the skin. If the anterior part of the head of a frog is cut off transversely just behind the eyes, the operation deprives the animal at once of retinal images and of its higher nervous centers. What is left of the animal still responds to light, but only through the skin and by means of a much simpler central apparatus than it had before the operation. Such a frog will maintain a natural sitting posture, and, if near a window, it will turn till it faces the light, after which it will commonly move forward from time to time toward the window. It is in no way excited by small moving objects about it, but it presents all the appearances of a simpler positively phototropic animal. Its transformation is most perfect and complete. Here, then, the influences that cover over and obscure the fundamental tropisms have been removed and the animal is reduced to that state which in a way was probably characteristic of its remote ancestry. Thus by a simple operation a highly complex vertebrate may be reduced to a simple tropic animal.

If this outline represents the true course of events, it follows that vertebrates react in ways other than tropic in consequence of their enriched sensory fields, whose details are relatively enormous as compared with those of the simpler animals. This is especially true of the retinal fields. Such enriched sensory relations have induced in these complex animals the development of a vastly intricate central nervous organ, and on these two elements, the complex field and the intricate center, are based the possibilities of the sensations, memories, volitions, and other like activities that give diversity to our performances as compared with those of the simpler animals. Though vertebrates show little of the primitive tropic responses, the insects afford interesting examples of balanced forms of behavior in which, though the tropism is clearly discernible, the higher type of response, the response to detail or what may be called the singular response, is clearly visible.

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